

Mammalian evolution in response to the Pleistocene-Holocene transition and the break-up of the mammoth steppe: two case studies

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Abstract. The Pleistocene-Holocene boundary, between 13-9 ka, seems to be one of the most informative times with regard to our understanding of rapid evolution in response to climatic change. This was a time of great faunal revolution for large mammals in particular, with tremendous distributional changes, rapid evolution, extinctions, and radical changes in community structure. At the time of the break-up of the Mammoth Steppe, the arid steppe which dominated from Alaska to England, some northern large mammals, like woolly mammoth, suffered from the reduction of solid footing and disappearing arid grasses and forbes. Other species, like moose, were favored by the climatic amelioration resulting in greater forestation and wetlands. These two species are emblematic of the conflicting repercussions of changing climates. The role of new human colonists moving into the north at this same time complicates our assessment of these climatic-mammalian interactions but new radiocarbon dates of moose and mammoth suggest that the interaction between humans and large mammals, while significant, was not the chief causal agent of the faunal revolution at this critical Pleistocene-Holocene transition.

Key words: Pleistocene, Holocene, moose, mammoth, climate, Alaska, Siberia.

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I. INTRODUCTION

The Pleistocene has been a tumultuous time in earth history, greatly affecting mammalian evolution, especially in the Holarctic. The essentials of appearance, physiology, and behavior of each mammalian species today can best be seen as an Ice Age legacy. Mammalian distributions, local faunal compositions, as well as recent extinction patterns are also best understood in terms of the climatic setting of the late Pleistocene. While that is a truism, the Holocene climate has also exerted its effects on mammalian evolution. In

this paper I will briefly review some ideas relating to the faunal events which occurred at the juncture of the Pleistocene with the Holocene.

Though not necessarily the most important faunal event in the Quaternary, nor the most dramatic, this associated climatic shift and faunal repercussion about 13-9 ka (centering around 12 ka) occur at a time which has the greatest meaning to humans and it is also a time for which we have most data because of its recency. I will focus especially on the northern Eurasian effects and the repercussions of these climatic changes for the Western Hemisphere. I have selected two large mammal species to differentiate between human impact and the effects of climatic change: the wide-spread Holarctic woolly mammoth, *Mammuthus primigenius*, which drastically decreased its geographic range at the beginning of the Holocene and ultimately became extinct, and moose, *Alces alces*, an insignificant Pleistocene species which expanded and flourished, extending its range into northern Asia and North America for the first time.

Ultimately, the climatic changes around 12 ka were extra-terrestrial in origin, relating to the perturbations of sun-earth relationships by the orbital geometry of Saturn and Jupiter. Over the first half of the Quaternary the major climatic patterns were dominated by the obliquity contribution, cycles of around 40,000 thousand years in duration, but about 0.7 ma climatic influences shifted toward a dominance of orbital eccentricity, that is, cycles of around 100 thousand years in duration. At the beginning of the Holocene, the earth began to experience a reduced eccentricity (which will continue until about 25,000 years into the future). This extreme circularity of the orbit during the Holocene is unique for the late Pleistocene, and I would argue that the climatic changes during the Holocene are very different from those which occurred in the slope into other recent Interglacials or Interstadials. It is important to note that the climatic perturbations from the 12 ka event were not limited to simple insolation changes, rather the repercussions secondarily diverted ocean currents and atmospheric circulation patterns, which had local effects far beyond the calculated changes in insolation value. The northern part of the globe, especially Eurasia, has been disproportionately affected by these eccentricity cycles, creating a quite different climatic and biotic environment during most of the Pleistocene than exists today, which I tried to capture in the concept of the *Mammoth Steppe* (GUTHRIE 1990a).

In earlier papers (GUTHRIE 1982, 1984a, 1984b, 1990a,b), I discussed the climatic forces across Eurasia which shifted the evolutionary balance in many Pleistocene ungulates (artiodactyls particularly) allowing them to become hypermorphic (large in body size with huge social organs such as horns and antlers). These climatic events seem to be an overall shift in the availability and digestibility of high quality forage during the growth season. More nutrients were available for body growth for a prolonged season. It seems that the more "plant-hostile" climate during most of the Pleistocene resulted in a carbon-nutrient balance shift toward a nutrient enrichment of plant tissue. One of the important forces behind this shift was the reduced summer cloud cover across the north which decreased net moisture input, increased evaporation and reduced snow cover lengthening the ungulate growth season. These climatic changes favored more arid forbes and grasses, low in antiherbivory compounds, which are the plants to which most grazers are adapted. Grazing caecalid perissodactyls and proboscideans (mammoths, rhinos, and equids) were

affected somewhat differently by these changes, though even among those forms, hyper-morphic growth was produced by mid-Pleistocene climatic conditions across Eurasia.

Cold arid Pleistocene conditions across the north placed energy limitations on plant growth. Plants with limited moisture and reduced temperature are unable to reach maximum growth, and as a result, characteristically have less energy (fiber-carbohydrate) in relation to nutrients. Also, atmospheric CO₂ was reduced during much of the cold-dry episodes, perhaps further shifting the balance toward the nutrient end of the equation. Less atmospheric CO₂ limits energy available to plants and means that plants grow less than their maximum potential. The CO₂ levels during full glacial were 180 ppm compared to over 300 ppm for the Holocene. The Pleistocene growth conditions of colder winters with reduced snow cover and cooler, windier summers without tree-cover add to energetic stress on plants. With these stresses on maximum growth, plants tend to not only cut back quantitatively on energy devoted to fiber-carbohydrate growth, but also do so qualitatively by allocating less to anti-herbivore defenses. This results in more digestible and more nutritious forage, for herbivore species adapted to those particular diets (MATTSON 1980; BRYANT et al 1983).

With thinly spread plant biomass and intense winter bottlenecks on the Mammoth Steppe, the carrying capacity of large mammals was reduced to medium-to-low levels meaning that each plant was less likely to be grazed during summer. Because most defense compounds are relatively energetically expensive, plants respond to long-term reduction in grazing with a reduction of anti-herbivory defenses. In sum, Pleistocene climates across northern Eurasia provided growth season resources which were more digestible and higher in nutrients for individual grazers, than at present. For every bite, the grazer gets more nutrients and as a result there seems to have been a shift to a more hypermorphic optimum.

While some mammals like mammoth, *Mammuthus* and bison, *Bison* thrive on this high quality arid grassland, some browsing ungulates, like roe deer, *Capreolus* and moose, *Alces*, are more adversely affected by these conditions. At around 12 ka, with the slide toward the Holocene, these norms were reversed. Instead, the general trend was a hypomorphic shift, decreased body size and reduced body decoration and social weaponry, for example, in animals like bison, *Bison* and red deer, *Cervus*. This paper is about a few evolutionary features which accompanied the climatic change at that time resulting from the break-up of the Mammoth Steppe.

II. THE UNIQUE FAUNAL REVOLUTION OF 12 000 YEARS AGO

One of the main difficulties presented by any attempt to analyze the climate-faunal interactions at the Pleistocene-Holocene boundary is the complicating factor of the exploding human numbers and their ecological influence (see MARTIN & KLEIN 1984). Among those influences is the haunting possibility that people were directly responsible for the megafaunal extinctions. Although this remains a possibility, it does not seem to explain the other accompanying faunal perturbations: (1) rapid and extensive distributional changes, (2) changes in community structure of new associations and arrangements,

(3) extremely rapid evolution within mammalian species (see GUTHRIE 1990b for a review).

Further complicating the separation of human and climatic influences on the biota, there seems to be an almost exact timing coincidence of human expansion and climatic shifts, presumably because the climatic-vegetational changes promoted human colonization and expansion at 12 ka. So, better and better dates themselves may not necessarily resolve the issue on such things as pinpointing the causes of the late Pleistocene megafaunal extinctions, though the pattern of these dates may. The nature and timing of human entry into North America is a major issue in New World prehistory. It is indeed a critical issue because of its implications for related matters in linguistics, evolutionary change, ecology, cultural adaptability, and faunal extinctions (see MARTIN & KLEIN 1984). Despite the presence of considerable data, this controversy still rages and has shown no sign of resolution. Whether there were people in North America who preceded the spectacular Clovis explosion shortly before 11 ka is a puzzle, but whatever the answer to that question, it is agreed that there was little detectable human impact on biota or landscape until Clovis times. One line of thought argues that the spread of Clovis traditions represents an actual colonization event and not simply a spreading technology. Yet, good technological precursors to Clovis occur in Alaskan sites a few hundred years prior to the appearance of Clovis in the mid-continent (HOFFecker et al. 1993), and only few very controversial archaeological sites in Alaska-Yukon date prior to 12 ka, so it seems logical that "Protoclovis" colonization of North America came from the Old World through Alaska at the end of the last glaciation. This pattern is a view accepted by the majority of Quaternary researchers, but not all (e.g. STANFORD 1991).

Remember that direct dating of human bones from the wave of first colonizers is near impossible because virtually no human bones have been found from this time range. We must instead date archaeological sites, the trace fossils – and this is where potential problems arise. Experience has shown that it is sometimes difficult to associate sound dates with sound artifacts. This is the source of a very real problem. Not only can archaeological sites sometimes be difficult to date, they may also be disturbed so that the wrong date is obtained. Also, it is often difficult to identify an artifact with assurance outside the proper context of a site. Sometimes correct identification is even insufficient, for example, in the north where frozen mammoth ivory is so abundant. Later peoples sometimes used this old ivory for ornamentation or tools – making reliable dates on acceptable artifacts misleading. There does seem to be a pattern of solid unquestionable dates in North America slightly after 12 ka. Those prior to that time all are problematic and controversial.

Despite the dramatic climatic and vegetational disruption at 12 ka, virtually no large mammals colonized North America from Asia. Humans have been considered unique in being the only species of large mammal to invade Siberia, cross the land bridge into Alaska, and on into continental North America at the end of the last glacial. However, emerging data in the last few years has shown that there is one exception to that statement, moose. Moose seem to have followed this same route into the New World at about the same time, and it would seem that its expansion in that same direction as humans was both restrained and encouraged by some of the same vegetational and ecological changes.

III. MOOSE – A CO-TRAVELER WITH HUMANS INTO THE NEW WORLD?

I submit then that moose was the only wild mammal which accompanied humans as they dispersed into the New World. Because moose normally lives in lowland "depositional" environments, its bones are relatively abundant in the fossil record, moose are, in fact, a good proxy indicator to gain new insights into human colonization of the New World. At this time we have solid evidence that, like humans, moose populations colonized northeastern Siberia at the end of the last glacial, expanded across the Bering land bridge into Alaska, on down the opening passageway between the Canadian Laurentide and Cordilleran ice sheets, then spread out into mid-continent North America, and expanded rapidly cross-continent to the Atlantic shores.

My thesis is the following: that moose and people seem to have been, rather indirectly and perhaps inadvertently, limited by some of the same forces. Both needed significant amounts of woody vegetation and a degree of climatic amelioration to operate. Moose are woodland and woodland edge animals and, the data suggest, anywhere moose could live, people with postglacial levels of technological sophistication could also. Moose cannot survive year-around on exposed windswept tundra or low shrublands without wooded cover. Woodland cover was apparently missing from northern Siberia and Alaska during the last glacial (HOPKINS et al. 1981) preventing both humans and moose from expanding into the windswept north (GUTHRIE 1990a). The paleontological and archaeological record of Northern Siberia shows this pattern clearly (GUTHRIE 1990b; HOFFECKER et al. 1993).

IV. MOOSE EVOLUTION AND CLIMATE

Like the controversy over human origins, the origin of moose as a species is not clear (e.g., AZZAROLI 1985; BUBENIK 1986); however, we can safely say that neither humans nor moose first arose in the New World. Moose are semi-aquatic deer and rely a great deal on pond vegetation and the willows that grow in lowlands. It has even been argued that they require aquatic vegetation to meet mineral requirements. I think it is most appropriate to see moose as primarily a water deer not as a snow adapted deer, that latter adaptation it seems is secondary. The exceptionally long legs with elastic tendons, elongate splayed hoofs, almost like sitatunga, *Tragelaphus spekei*, allowing feet to be withdrawn vertically from deep mud and the elaborate nasal structure which allows moose to browse on water plants deeply beneath the pond surface, all seem to be specialized aquatic adaptations. These are present to a lesser degree in the Pleistocene ancestral genus *Cervalces*. Though it is not clear where *Alces alces* arose or exactly when, it is rare as a Pleistocene fossil anywhere, and particularly during the last full glacial (isotope stage 2, around 25-16 ka). However, it expands rapidly in distribution, and apparently in numbers, in Holocene times to dominate the boreal forest all across Eurasia and North America, and becomes quite common in the fossil record. We can assume that *Cervalces latifrons* (some refer this species to *Alces latifrons*) was present in Alaska (and probably in Siberia as well) during the interstage (isotope stage 3, around about 40-28 ka) from several dated specimens (GUTHRIE 1990c).

Earlier in the Quaternary *Cervalces* had established itself in the far north and invaded North America, where it evolved into the very bizarrely antlered stag-moose, *Cervalces scotti*. Though there are a number of *Cervalces* skulls and antlers from Alaska, none are *C. scotti*, so there is no evidence that *C. scotti* ever recolonized Alaska from the south.

Originally it was thought that moose, *Alces alces*, occurred south of the ice sheet during the last glaciation and that glaciation served as an isolating mechanism creating four subspecies of North American moose (PETERSON 1955; KELSALL & TELFER 1974; GASAWAY et al. 1987). Though this seemed logical, it would have meant that moose existed sympatrically with a close phylogenetic and ecological equivalent, *Cervalces scotti*, during the peak of the last glaciation. Though possible, this was unlikely, and caused paleomammalogists to examine the data more closely (KURTÉN & ANDERSON 1980). No Pleistocene moose fossils have yet been found south of the ice sheet, so it is now assumed that they are indeed a Holocene immigrant, arriving at about the time *Cervalces scotti* became extinct (CHURCHER & PINSOFF 1987; GEIST 1987).

In a similar pattern of conceptual change, it was assumed that moose populations were present in Beringia during or prior to the last glacial maximum (PETERSON 1955; GASAWAY et al. 1987). However, pollen and mammalian fossil evidence began to show a treeless grassland predominating in this region (see GUTHRIE 1990a for a review), making it very unlikely that an almost obligate browser like moose could have survived. Dates from *Cervalces* in Alaska (GUTHRIE 1990c) supported the one date from the Yukon Territory (HARRINGTON 1978) showing that *Cervalces* (*Alces latifrons*) occurred there as late as the warm interstade within the last glaciation (c. 35 ka) and not during the full glacial centering around 18 ka (GUTHRIE 1990c). Since no *Cervalces* specimens are known to occur anywhere in Postglacial times, the only species which could have colonized Beringia at the end of the last glaciation was *Alces alces* not *Cervalces* (*Alces latifrons*). Thus, it has only become clear in the past few years that moose had paralleled the postglacial expansion of humans into the Western Hemisphere. The four moose subspecies in north America seem to represent rapid evolution as well as developmental plasticity (GEIST 1987).

Recent mitochondrial genetic information for moose confirms the above assessment, of very late colonization into North America, because the mtDNA samples of moose from various parts of North America showed no mtDNA polymorphs, at least outside the D-loop, suggesting a very recent origin and close kinship of all North American moose populations (CRONIN 1989, 1991). Unlike caribou, adult male moose do not seem to be wholly adapted to the severe winter temperatures of the subarctic. For example, a high percentage of senior moose bulls in Alaska have the long tail of the ventral neck bell missing. This appendage freezes off when the bulls first begin to actively participate in rut, using up most of their fat reserves for winter, which probably forces them to restrict peripheral circulation in the coldest weather as a heat conservation strategy. Moose bulls to the south, say, in British Columbia, do not lose this part of their bell to freezing.

During the last Glacial, the expanding cold arid Mammoth Steppe across northern Eurasia drove the boreal forest far to the south. As in North America, old forest complexes disintegrated as species behaved individualistically and recombined into a number of

diverse communities without modern analogues. We can assume that, being tied to this woody browse, moose were also driven far to the south in Eurasia during the full glacial (for example, there is not a single moose pictured in the thousands of large mammal portrayals in Pleistocene Paleolithic art in the Franco-Cantabrian region). There is growing acceptance that Eurasian people were also driven into southern Eurasia by the cold climate (see GAMBLE & SOFFER 1990). I have suggested (GUTHRIE 1990a) that while the forces were probably complex, one particular deficiency keeping humans out of the far north was the climatically induced absence of the boreal forest fringes for protection from the high chill-factors of this special continental region and the lack of significant wood to burn for heat. The lack of boreal forests affected moose in similar ways, but for somewhat different reasons. Moose are browsers, relying mainly on riparian willows and boreal forest trees, especially the successional hardwoods in old burns. While they can venture well beyond tree-line they ultimately require significant woodland conditions, at least substantial willow riparian fingers, for long-term occupation.

With the late Glacial climatic amelioration of increased cloud cover (the reduction of the intense summer high pressure area over central Siberia), the boreal forest recolonized the far north. This seems to have been a critical part of moose, and human, colonization northward. Pollen profiles from lake cores in Northern Siberia are in their early stages of study and this will provide more precise chronologies on the timing of reforestation than we have in hand. But the preliminary information as to the timing of the Asian boreal forest expansion suggested that it was centered around 11-14 ka (about the same as in Alaska).

The issue is when did moose arrive from Asia into the Alaskan gateway to North America; that is, when were moose there, ready to move southward through the corridor? Recent information on sea level changes (ELIAS et al. 1992) shows a much later date (around 10 ka) of flooding of the Bering Strait rather than the previous date around 12 ka (Fig. 1). This overcomes the problem of people or moose arriving northward with the first tree outliers and being unable to beat the rising seawater separating the two hemispheres. We now can assume that the population perimeter of both moose and people expanded from Siberia into North America dry shod. However, no boreal forest mammals, such as, American red squirrel, *Tamiasciurus*, or porcupine, *Erethizon*, etc., arrived in time to make this crossing, suggesting that moose and people were expanding on the forward edge, with the boreal forest hardwoods. These hardwoods preceded the invasion of conifers, well ahead of the present boreal forest physiognomic complex.

Northern colonization affected moose evolution. Wyoming moose are a monotone gray in body color, while the eastern Siberian and Alaskan-Yukon moose are highly marked in blacks and tans; these latter are extremely large and have enormous antlers. This selection for hypermorphic traits seems to have been the product of excellent summer forage for moose: pond vegetation, thick stream willows, and other deciduous fire successional growth, to which this aquatic deer is adapted. Severe winters with occasional years of deep snow and large wolf packs keep moose populations comparatively low, creating little summer competition for high-quality and easily digestible forage, necessary for large body size. However, when moose move south into mid-continent conditions they again come into temperate climatic conditions and experience rapid hypomorphic evolutionary

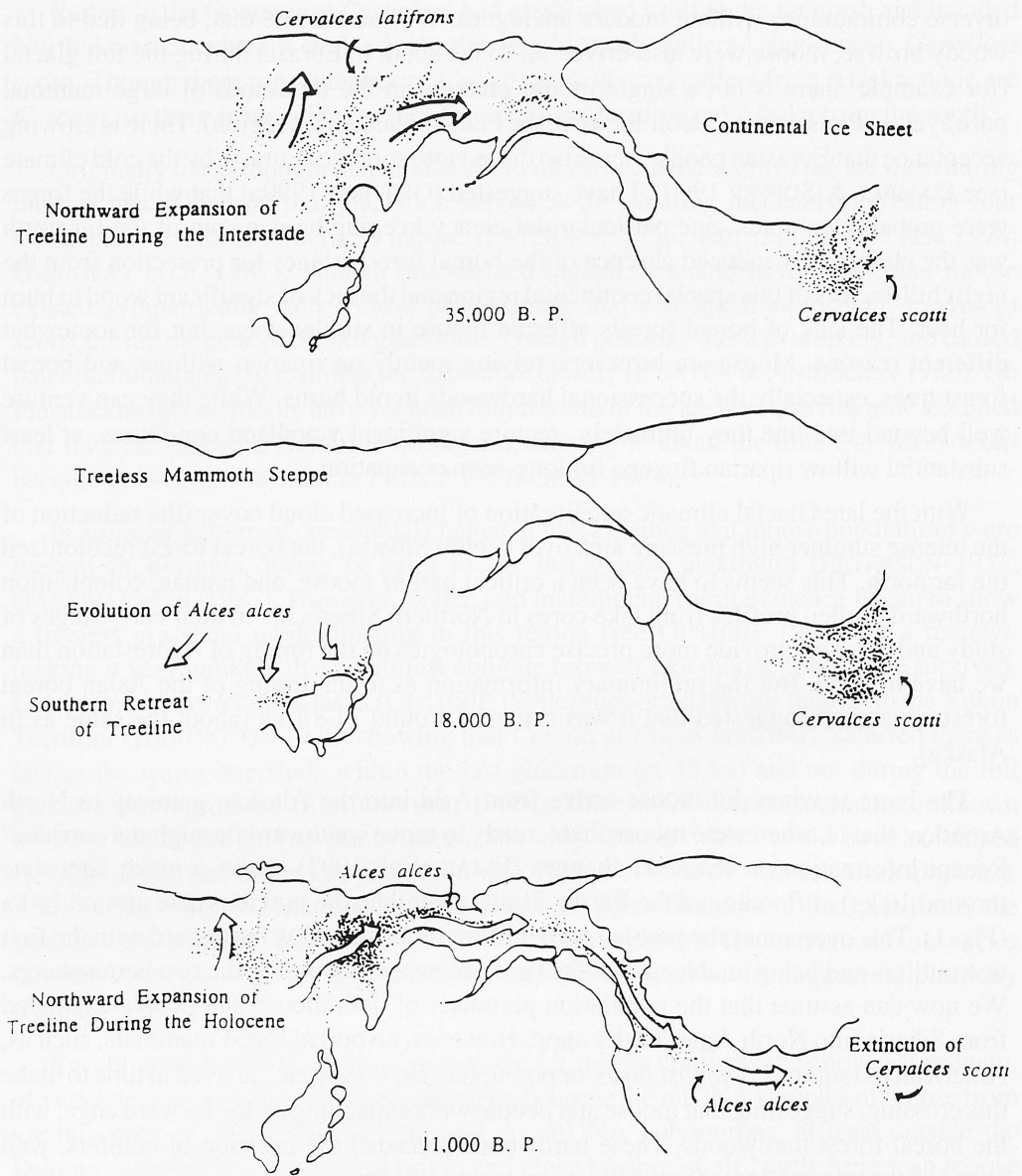


Fig. 1. A theoretical model of *Alces* and *Cervalces* (*Alces latifrons*) distributions, extinction, and evolution in relation to late Pleistocene climatic changes.

changes. Moose of Southern Yakutia, Europe, and Wyoming are comparatively small bodied and are small antlered.

Once moose were in Alaska how long was it before they extended their range into Canada and through the corridor southward? The nature and timing of this Canadian passage has been the focus of considerable argument, with models ranging from an

impenetrable periglacial wasteland to a freely traversable corridor open any time except perhaps the thousand or two years around glacial maximum (see CATTO & MANDRYK 1990). We need more dates, but the information we have, suggests that moose may have made it south about the same time as people, prior to 11 ka.

V. THE TWO EXTINCTION THEORIES FOR WOOLLY MAMMOTHS, THEIR PROS AND CONS IN SHORT

Woolly mammoths are the kingpin of our Pleistocene image of these extinct northern faunas, as indeed they should be, for if it can be shown that mammoth were driven to extinction by human predation, we can easily imagine how other species also suffered with human predation. And the reciprocal, if we can attribute mammoth extinction to range reduction it suggests that the crescendo of late Pleistocene extinctions may also be attributable to those causes. That is why woolly mammoths are so important.

There is a variety of extinction theories but they seem to fall into two basic camps. The human overkill theory proposes that early human colonists into the New World at the end of the Pleistocene, were efficient big-game hunters and could kill large game faster than it could replace itself. Hence, it was humans which were directly responsible for the demise of many species of large mammals. The blitzkrieg version pictures the colonization wave from Asia as the expansion of Clovis artifacts. To circumvent the ecological problem that any species of large mammals kept below its carrying capacity greatly increases its reproduction, MARTIN (1984) has proposed a high-density human colonization wave (hence the *blitzkrieg* part of the model) of critical mass sweeping across the far north of Eurasia into North America and on to South America killing almost all large mammals.

The strength of the human overkill theory is its elegance and simplicity. Human expansion into North America does seem to coincide to a great extent with the extinction timing of such large mammals as mammoth. And, indeed, some of the extinct Pleistocene animal remains, mastodon, *Mammut*, camel, *Camelops*, etc., are found associated with human kill sites. Also this overkill model is consistent with the continued pattern of well-documented human caused extinctions on New Zealand, Madagascar, and throughout the world, in both prehistoric and historic times.

However, what has discouraged the universal acceptance of the blitzkrieg model is the fact that many of the extinct species are not associated with human archaeological sites, and seem to have become extinct before Clovis cultures arrived into the New World (GRAYSON 1991). For some researchers, it is inconceivable that people could have killed off so many creatures so fast, but of course it is a different time, involving different organisms, and different people than those with which we are familiar. So, our sense of "uniformitarianism" is at risk.

The other theory, the ecological explanation, has an equal number of problems. One of the factors which argues against any ecological theory of extinctions for so many diverse large mammal species is its complexity and inelegance. The evidence is for complex habitats and diverse large mammal communities in the Pleistocene with no modern analogs (GUTHRIE 1984a; GRAHAM & LUNDELIUS 1984). These ideas, that the present Holocene

is a radically different climate than virtually any other time in the Pleistocene, is based mainly on radically different faunal and floral associations in the past which are not found today (GRAHAM 1990). The argument proposed by the ecological theory is that vegetational changes occurred very rapidly, at 11-12 ka, too rapidly for many species to adjust. Yet this change favored many species, e.g. American bison, *Bison bison*, and moose, while restricting the distribution of many others, e.g. saiga, *Saiga tatarica*, and musk oxen, *Ovibos moschatus*. Ecological theorists simply picture some of these restricted distributions as being driven to zero, complete extinction. However, there are several versions of this ecological theory by different authors. The exact forces remain unfocused and unclear, while indeed it cannot be challenged that this was a turbulent time both climatically and biotically, what I have called a time of major faunal revolutions (GUTHRIE 1990b), ecological forces which could have created global extinction patterns are not easy to identify.

Both the overkill and ecological theories have a number of different versions championed by a variety of investigators. OWEN-SMITH (1987, 1988) has argued for a different twist to the human overkill theory. His contention is that megaherbivores (those species weighing over 1000 kg) are critical forces in maintaining community diversity and when they are removed the vegetation shifts into a more simplified pattern. As such, he argues they act as a "keystone," species, and when removed the whole integrity of the community collapses. Indeed, this does seem to occur for places in Africa, when elephant, rhino, and hippo are removed. And this keystone effect, in some ecological situations, seems to be a real phenomenon (BROWN & HESKE 1990; NAIMAN 1988). OWEN-SMITH's theory, of course, encompasses human overkill and at the same time explains the simplification of the vegetational communities, an important ingredient of the ecological extinction theorists argument. However, while this idea works for browsing elephants it is not easy to see how it would work for woolly mammoths (GUTHRIE 1990a).

New dates from Siberia do throw evidence in the direction of the ecological interpretation. If megafaunal extinctions were a product of the new human immigrants into northeastern Siberia, on into Alaska, then on into central North America, we would predict that the mammalian extinction wave, for such a species like woolly mammoth, kept in step with that same colonization pattern in a chronological sequence – moved in that same direction (Fig. 2). If, on the other hand, the megafaunal extinctions were due to a shift in vegetation patterns, then the extinction wave would predictably follow a south-to-north pattern, just opposite the direction of human colonization (Fig. 3). That is, a pattern of extinctions showing a south-north movement in North America, as in Siberia, lingering in known vegetational refugia, would indicate the extinction was most probably the result of a climatic-vegetational shift. That is the main direction of the vegetational colonization wave (HOPKINS 1982). Thus, the two theories would predict two very different patterns of extinction-wave direction in Alaska and Canada.

A recent mass dating program of Siberian mammoth fossils does reveal a pattern of woolly mammoth extinction in the northwestern part of Asia. It was clearly northward (VARTANYAN et al. 1992). However, the direction of the extinction wave in northeastern Siberia does not settle the issue of the role played by Paleolithic hunters. The reason is that in Siberia both the colonizing woodlands and human colonists were moving north-

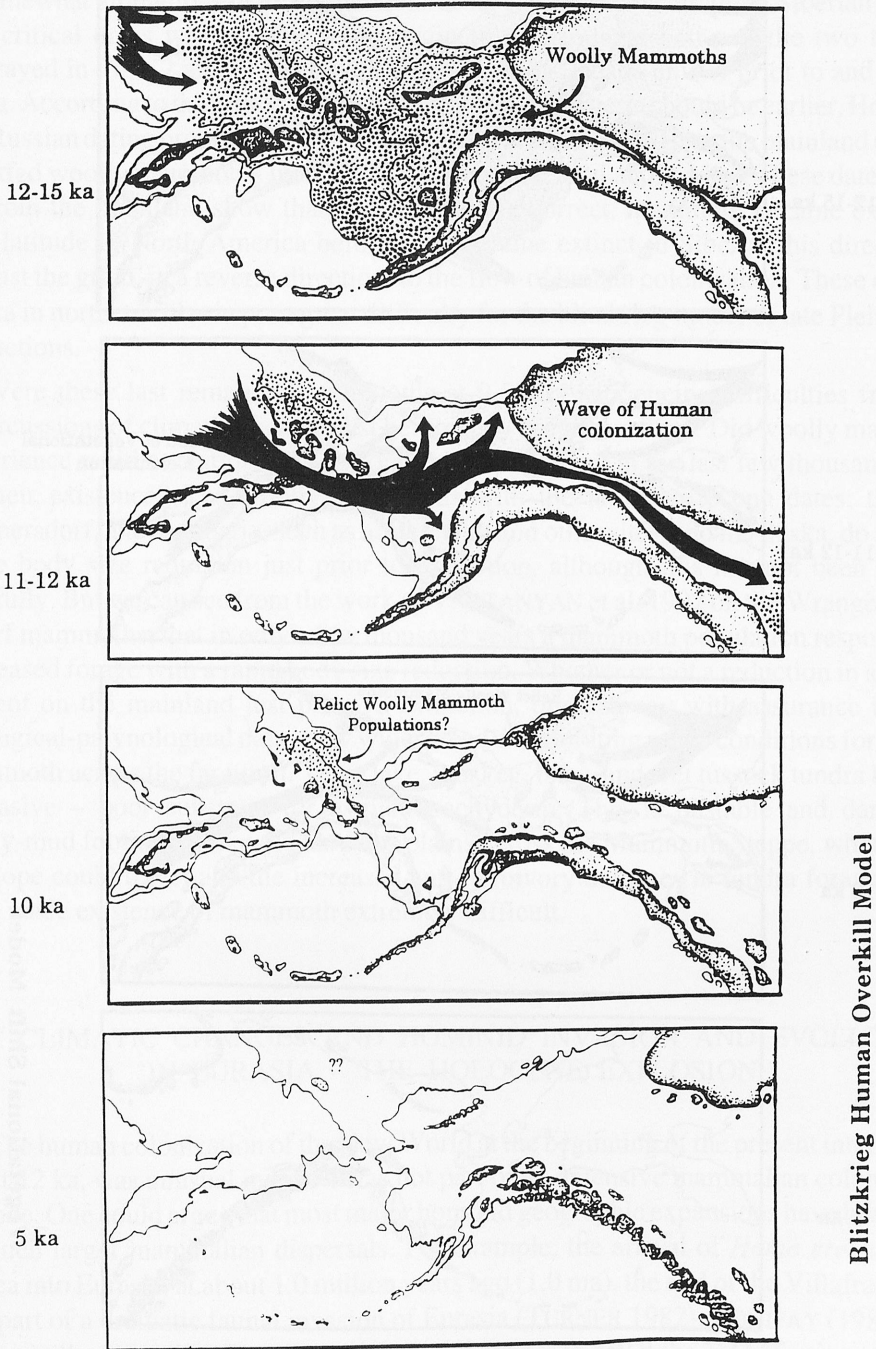


Fig. 2. The blitzkrieg model of woolly mammoth decline and extinction as caused by human colonizers from Eurasia. According to this model the wave of mammoth extinction should follow people colonizing northward into Siberia, then moving southward into North America. Thus the extinction pattern should lie along an axis from Siberia to Montana.

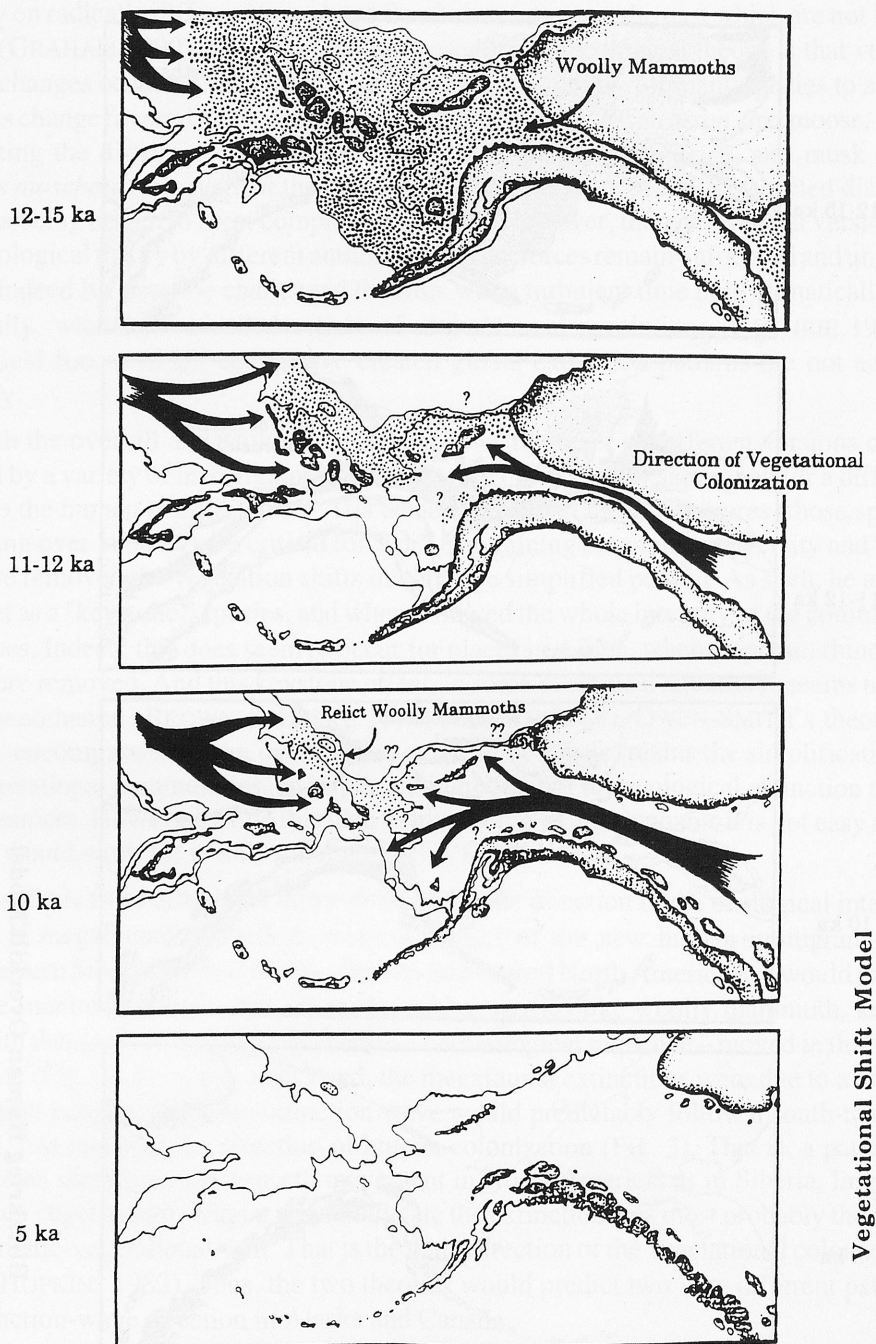


Fig. 3. The climate-ecological model of woolly mammoth decline and extinction due to changes in the vegetation community. According to this model, the wave of mammoth extinction should occur on a south-north directional pattern in both hemispheres. Plant communities seemed to have changed along in a time-transgressive gradient from south to north in North America as well as in Siberia.

eastward, in the same direction. So the northward pattern of mammoth decline in Siberia is somewhat ambiguous in its implications as its causes. However, these Siberian data do add critical dates which allow us to begin to discriminate between the two theories portrayed in Figs. 2 and 3. Mammoth dates south of Canada cluster prior to and around 11 ka. According to the blitzkrieg model all the dates in Siberia should be earlier. However, the Russian dating program did contain two dates around 9.5 ka from the mainland (insular dwarfed woolly mammoths lived in that same region until about 4 ka). These dates of 9.5 ka from the mainland show that, if the dates are correct, mammoth became extinct at mid-latitude in North America before they became extinct in Siberia, this direction is against the grain, in a reverse direction, to the flow of human colonization. These dates of 9.5 ka in northern Siberia pose great difficulty for the blitzkrieg model of late Pleistocene extinctions.

Were these last remaining mammoths at 9.5 ka experiencing difficulties from the repercussions of climatic changes just before they became extinct? Did woolly mammoth experience rapid evolution for a hypomorphic body form in the last few thousand years of their existence? The woolly mammoths with the late Pleistocene dates: those at Gönnersdorf, and in Siberia, such as at Berelekh and other sites, and in Alaska, do suggest some body size reduction just prior to extinction, although this has not been studied carefully. But we can see from the work of VARTANYAN et al. 1992 on the Wrangel Island dwarf mammoths, that in only a few thousand years a mammoth population responded to decreased forage with a rapid body size reduction. Whether or not a reduction in size was present on the mainland just prior to extinction, one can say with assurance that the geological-palynological data show widespread deteriorating range conditions for woolly mammoth across the far north. Thaw lake, muskeg, bogs, and wet tussock tundra become pervasive – poor substrate for a giant pachyderm. This is unstable and dangerous sticky-mud footing, unlike the hard dry plains across the Mammoth Steppe, where saiga antelope could travel and the increased anti-herbivory defenses in tundra forage would have made existence of mammoth extremely difficult.

VI. CLIMATIC CHANGES AND HOMINID INVASION AND EVOLUTION IN EURASIA – THE HOLOCENE EXPLOSION

The human colonization of the New World at the beginning of the present interstadial, about 12 ka, was unusual in that it was not part of an extensive mammalian colonization episode. One could argue that most major hominid geographic expansions have been parts of much larger mammalian dispersals. For example, the arrival of *Homo erectus* from Africa into Eurasia, at about 1.0 million years ago (1.0 ma), the end of the Villafranchian, was part of a dramatic faunal invasion of Eurasia (TURNER 1982). BONIFAY (1987) sees 1.0 ma as the most significant break-point and wishes to call it the T-Q (Tertiary-Quaternary) boundary. This climatic shift is seen almost everywhere on earth, even proxy data from underneath the Arctic Ocean ice-cap (HERMAN 1987). The loess formation which began much earlier in Central Asia, surges at 1.0 ma (DODONOV 1987). Tectonism throughout the globe seems to have peaked at this general time (AZZAROLI 1983). A peak

in erosion occurs at 1.0 ma and is called the Cassian phase (AZZAROLI et al. 1988). Thus, it seems that ecological changes directly influenced this "dispersal event," human range expansion being part of a larger phenomenon.

The same is true in a lesser degree during the last interstade (isotope stage 3), from 50 ka to about 25 ka, called the Upton Warren Interglacial in England. The peak of climatic amelioration occurred at around 40 ka. This interstade is a time when anatomically modern peoples invaded Europe and most of Asia, including Australia. Though not such a massive faunal revolution as some previous ones, the human expansions were again accompanied in Eurasia by several other mammalian species (STUART 1982), notably saiga antelope. This warming time is considered in Siberia as a true Interglacial as it was marked by widespread and dramatic change in flora and fauna.

I have proposed that the evolution of human subspecies formation occurred shortly after this interstade peak around 40 ka but achieved its extreme development during peak glacial, around 18 ka, and continued on into the Holocene (GUTHRIE in press), directed mainly by local environmental repercussions of these climatic changes. Neo-Mongoloids, the main colonizers of the Asiatic and American far north, seem to have attained their northern adaptations during the last Glacial in the lee of the Indian Monsoon, the cold-dry high steppes behind the Himalayas. These adaptations include thick epidermis, physiological cold tolerance, even distribution of subcutaneous body fat, fatty insulated eye fold, fatty facial insulating pad, reduced fat depots in breasts and buttocks, and a massive jaw-dental complex compensating for increased food consumption to meet the expenditure of greater calories. These include complex anterior teeth (shovel shaped incisors, enlarged premolars, complex first molars), enlarged jaw muscles, forward arrangement of temporalis muscle, flared jaw angles, and expanded zygomatic space. Mongoloid evolutionary changes developed during the peak glacial further south and their accompanying technological innovations allowed humans to colonize into the Arctic immediately upon the first opportunity at the end of the Pleistocene.

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